Estimating the impact of disease in species threatened by amphibian chytrid fungus: Comment on Murray et al.

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Abstract: Chytridiomycosis is an emerging disease of amphibians caused by the chytrid fungus Batrachochytrium dendrobatidis (hereafter Bd) (Fisher et al. 2009). Chytridiomycosis is thought to be contributing significantly to global amphibian declines (Berger et al. 1998; Stuart et al. 2004; Skerratt et al. 2007). In the Neotropics the disease has spread in a wave-like fashion (Lips et al. 2008), and arrival at previously pathogen-free sites in this region results in mass mortalities and extinctions (Lips et al. 2008). Little is known, however, about the effects of Bd after population declines have occurred. In some places, Bd persists where it has invaded (Retallick et al. 2004). Thus, amphibians may evolve resistance to this novel pathogen such that the negative effects of Bd are attenuated over time. Murray et al. (2009) address this very important question. They used a multistate mark-recapture model to estimate survival of Bd-infected and Bd-free frogs (Litoria pearsoniana) in Queensland, where Bd has been present for 30 years. The use ofmark-recapturemethods is a clear improvement over earlier studies in which survival was estimated but did not account for imperfect detectability of animals in field studies (Faustino et al. 2004; Schmidt 2004). Murray et al. found that Bd causes a substantial reduction in survival. This matters because a reduction in adult survival can lead to amphibian population declines (Schmidt et al. 2005) and because it implies that Bd remains a dangerous pathogen, such that amphibian populations are unlikely to recover from population declines caused by Bd for many decades, if ever. Here, I point out that the apparent monthly survival estimates ofMurray et al. are likely confoundedwith perma- Paper submitted November 11, 2009; revised manuscript accepted December 14, 2009. nent emigration from the study site (Sandercock 2006). If infected and uninfected frogs have different emigration probabilities, then one would obtain different apparent survival estimates from the mark-recapture analysis for Bd-positive and Bd-negative frogs.

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Comment

Estimating the Impact of Disease in Species Threatened by Amphibian Chytrid Fungus: Comment on Murray et al.

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Introduction

Chytridiomycosis is an emerging disease of amphibians caused by the chytrid fungus *Batrachochytrium dendrobatidis* (hereafter Bd) (Fisher et al. 2009). Chytridiomycosis is thought to be contributing significantly to global amphibian declines (Berger et al. 1998; Stuart et al. 2004; Skerratt et al. 2007). In the Neotropics the disease has spread in a wave-like fashion (Lips et al. 2008), and arrival at previously pathogen-free sites in this region results in mass mortalities and extinctions (Lips et al. 2008). Little is known, however, about the effects of Bd after population declines have occurred. In some places, Bd persists where it has invaded (Retallick et al. 2004). Thus, amphibians may evolve resistance to this novel pathogen such that the negative effects of Bd are attenuated over time.

Murray et al. (2009) address this very important question. They used a multistate mark-recapture model to estimate survival of Bd-infected and Bd-free frogs (*Litoria pearsoniana*) in Queensland, where Bd has been present for 30 years. The use of mark-recapture methods is a clear improvement over earlier studies in which survival was estimated but did not account for imperfect detectability of animals in field studies (Faustino et al. 2004; Schmidt 2004). Murray et al. found that Bd causes a substantial reduction in survival. This matters because a reduction in adult survival can lead to amphibian population declines (Schmidt et al. 2005) and because it implies that Bd remains a dangerous pathogen, such that amphibian populations are unlikely to recover from population declines caused by Bd for many decades, if ever.

Here, I point out that the apparent monthly survival estimates of Murray et al. are likely confounded with permanent emigration from the study site (Sandercock 2006). If infected and uninfected frogs have different emigration probabilities, then one would obtain different apparent survival estimates from the mark-recapture analysis for Bd-positive and Bd-negative frogs.

Emigration Versus Survival

My argument is based on the following assumptions: mark-recapture survival estimates are estimates of apparent survival (i.e., survival on the study site), the study site is much smaller than the home range of the frogs, calling and reproduction are activities that are energetically costly, infected and uninfected frogs may have different energy reserves or less energy may be allocated to reproduction and calling (and invested into immunity instead) in infected frogs, infected and uninfected frogs may have different permanent emigration probabilities.

Mark-recapture models estimate apparent survival. More precisely, they do not estimate true survival probabilities but rather the following product: true survival $\times$ (1 $-$ probability of emigration) (Sandercock 2006). Although in many studies emigration is likely to be negligible, and apparent survival reflects true survival, in other studies it is likely that mortality is negligible and apparent survival reflects residence time at a place (Schaub et al. 2001). Without some auxiliary information it is impossible to disentangle true survival and emigration. Auxiliary information may actually help estimate emigration probabilities (Schmidt et al. 2007).

Murray et al. estimated monthly apparent survival from October 2006 to February 2007. This period covers the entire active (i.e., breeding) season of the frogs.

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If one multiplies all monthly apparent survival estimates, then one obtains an estimate of apparent survival for the entire active season of the frogs. In Murray et al., for Bd-positive frogs that remain positive, apparent survival across the entire season is approximately $0.1 \times 0.2 \times 0.25 \times 0.3 \times 0.6$ (these values are rough estimates derived from Fig. 2a of Murray et al.). Thus, about 0.09% of the infected frogs that were present at the start of the active season survive the active season. This is an extremely low proportion.

Emigration may explain why cumulative apparent survival across the season is low. In Murray et al.'s study, frogs were captured along a 120-m stream transect. Thus, the study site probably covers only a small proportion of the annual home range of the frogs. The frogs may have easily left the study site and are thus considered dead by the mark-recapture model. In context of the study, emigration does not necessarily mean dispersal between populations but simply that frogs permanently leave the study site. Interestingly, Murray et al. did not analyze data from female frogs because females stayed at the stream for even shorter periods. Results from other studies of hylid frogs show that males do not stay at the breeding site for the entire season (Friedl & Klump 2005; Grafe & Meuche 2005). Thus, if the study site is the breeding site, frogs are likely to leave the study site and may return the following year.

Calling and reproduction are energy-consuming activities (Grafe & Thein 2001). Male frogs that must fight a pathogen may have less energy available for reproduction (McCallum & Trauth 2007) and thus may be exhausted and leave the breeding site after a shorter stay than uninfected frogs. It thus seems likely that male frogs that carry a pathogen spend less time at the stream. This would then lead to different emigration probabilities between infected and uninfected frogs, which would lead to a spurious difference in survival probabilities.

Murray et al. present data on movement. They report that frogs usually do not move much. This, however, does not exclude the possibility that frogs emigrated permanently from the study site. The movement data of Murray et al. only refer to frogs that stay on the study site and that were recaptured; it cannot be used to infer movement of frogs that were never recaptured.

Conclusion

Murray et al.'s results show that apparent survival probabilities depend on infection status of the frogs. It is not possible, however, to disentangle the relative contributions of true survival and emigration. Both may contribute to the difference in true survival between infected and uninfected frogs. Because apparent survival across the entire active season is very low, I believe most of the difference is caused by permanent emigration from the study site. Morrison (2001) estimated monthly survival during the breeding season of *Litoria pearsoniana* and found that at one site it was as high as 0.9509 (95% CI 0.0112–0.9999), although the estimate for another site was as low as 0.1433 (95% CI 0.0537–0.2328). In a multiyear mark-recapture study, Retallick et al. (2004) did not find consistent effects of Bd on apparent frog survival. With multiple years of data, emigration from the study site within a season does not necessarily lead to a confounding of survival and emigration because frogs can be recaptured in the following year when they return to the study site.

Even if no permanent within-season emigration from the study site occurs, Bd-induced mortality may not affect population dynamics much. *Litoria pearsoniana* males may be very short lived (Morrison et al. 2004). Morrison et al. (2004) found that most frogs ($n = 187$) were 2 years old. There were only four 1-year-old males and no 3-year-old males. There were also no recaptures in subsequent years. This means all frogs, both those Bd-positive and those Bd-negative, will die after a single breeding season. If Bd leads to an earlier death of frogs that would have died anyway, then this is unlikely to affect population dynamics much.

Nevertheless, Murray et al. found that Bd still has an effect on frog populations decades after it has emerged in the host. Because Bd either affects within-season survival or reproductive activity, this means Bd remains a virulent pathogen to which the frogs are still susceptible. The obvious next step is to identify which of these effects is important in causing these observed differences in apparent survival and how this affects population viability.

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